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THE BIGCONE DOUGLAS-FIR—CANYON LIVE OAK COMMUNITY IN SOUTHERN CALIFORNIA

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Little is known about the ecology of bigcone Douglas-fir [*Pseudotsuga macrocarpa* (Vasey) Mayr]. Its relations to tree associates, soils, topography, and habitat are at best poorly understood. Whether or not bigcone Douglas-fir occupies a dominant or subordinate position within its habitat is not well known. Is it regenerating and invading new areas vigorously, holding its own, or losing ground?

Various workers have described the location, silvics, and habitat of bigcone Douglas-fir. Mason (1927) included bigcone Douglas-fir in his California Coast Range Forest, considering it an endemic and relict species. Sudworth (1908) described the natural range of the species as being delimited by lack of moisture at low elevations and by severity of climate at high ones. Furthermore, the species grows on sites too shallow, rocky, or dry for most other conifers.

In his study of vegetational types of the San Bernardino Mountains, Horton (1960) considered bigcone Douglas-fir to be a member of two vegetation types: (1) a Live Oak Woodland and (2) a bigcone Douglas-fir type. The Live Oak Woodland type usually is found on north slopes, where canyon live oak (*Quercus chrysolepis* Liebm.) predominates, although scattered individuals of bigcone Douglas-fir are often found. Bigcone Douglas-fir dominates in its type, but canyon live oak usually is present. Dominance of bigcone Douglas-fir often is reduced by fire. "Those portions of the bigcone Douglas-fir forest that are destroyed are replaced by live oak woodland or live oak chaparral and the return of the bigcone Douglas-fir probably requires centuries" (Horton, 1960).

Gause (1966) pointed out the necessity of shade for bigcone Douglas-fir seedling establishment such that with time, continuous shade becomes a liability. A span of 40–70 years commonly is required for this species to penetrate through 5 to 9 m overstories of canyon live oak.

Methods

We sampled bigcone Douglas-fir throughout much of its range during 1966–1970. Sample locations ranged from near Tejón Pass (Los Angeles County) to near its southerly limit in California in the Agua Tibia Mountains (San Diego County), and from the San Bernardino Mountains to Tejón Pass and the west slopes of the Santa Ana Mountains. The known elevational range (280 to 2400 m) of bigcone Douglas-fir also was spanned intentionally by the samples. Altogether, 16 locations (stands) were chosen (fig. 1).

At each stand, from 4 to 12 rectangular transects 1.8 m wide and 30.5 m long were established. At least one bigcone Douglas-fir had to be

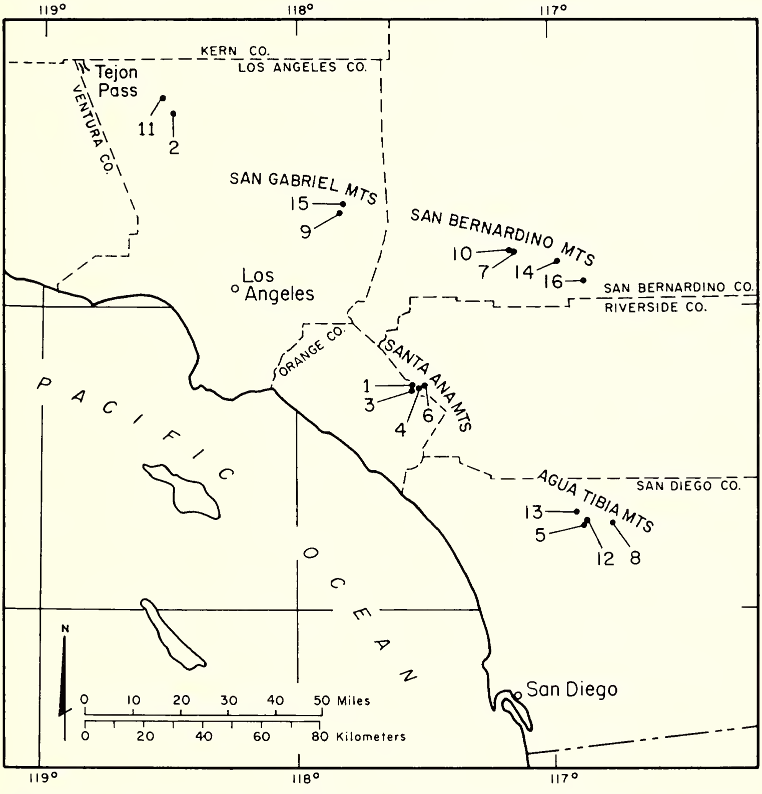

FIG. 1. Location of sampled bigcone Douglas-fir stands. (Stand numbers increase with increasing elevation.)

present on each transect. Transects were chosen, albeit arbitrarily, so that the tree community about bigcone Douglas-fir would have the best chance of being represented. Although edge effects and ecotones were avoided when recognized, the transects were located without a preconceived notion of what the community would be.

The number and orientation of the transects depended on vegetation and topography. A stand in a narrow canyon was sampled best by a few transects angled obliquely to the canyon floor. Vegetation at the bottom of a sloping hillside was measured by additional transects, one or two of which would be joined together lengthwise. Where the terrain was less steep and the vegetation more open, we selected a larger number of transects. Here their orientation resembled line transects from 122 to 183 m long. Altogether, 90 transects were established.

All regeneration (seedlings from 1.0 to 30.5 cm tall), advance reproduction [plants from 3.7 cm tall to 2.5 cm in diameter at breast height (d.b.h.) 1.4 m above mean ground line], and trees (2.8 cm d.b.h. and larger) were recorded along each transect. Data were converted to density and basal area for each stand. Subjective data included presence of acorns, cones, and woody plants, number of stems per clone, and seedling growth rates.

Climate of the canyons and slopes where bigcone Douglas-fir was sampled is typical of the species habitat. Precipitation falls mostly in winter, seldom in summer. Annual precipitation ranges from 356 to 1016 mm. On windward slopes, precipitation increases with elevation. For example, in the San Bernardino Mountains annual precipitation at Santa Ana River Powerhouse number 3 (elev. 843 m) is 378 mm, at Mill Creek intake (elev. 1512 m) 654 mm, and at Running Springs (elev. 1819 m) 931 mm (U. S. Weather Bureau, 1964).

Temperatures throughout the study area are moderate and warm. Mean annual temperature is about 14°C. Extreme high and low temperatures are 41°C and −12°C. Even winter months can be warm (Sinclair et al., 1953), and in some years at least one of the winter months can be warmer than May or June (Hellmers, 1959).

The 16 sample stands represented the species over a wide range of physiographic conditions. Elevations ranged from 732 m to 1830 m. Slopes varied from 1 to 93 percent, and numerous aspects were represented.

Various soil characteristics such as color, depth, texture, and parent material were physically noted for each stand and then referred to a geology text for southern California (Jahns, 1954), the Geologic Map of California (Calif. Dept. Natur. Resour., 1955; 1965; 1967), and to soil series. California soil series are identified by the California Cooperative Soil-Vegetation Survey and the National Cooperative Soil Survey.

In this report, relationships are presented individually for bigcone Douglas-fir, canyon live oak, and "associated" species. "Associated" collectively means all tree species except bigcone Douglas-fir and canyon live oak. We further subdivided the tree category into various diameter classes and recorded the number of stands in each.

Results

Elevational Gradients. Trees accompanying bigcone Douglas-fir were divided about evenly between conifers and hardwoods. As associates, each occupied a fairly distinct elevational range (fig. 2).

Where present, bigcone Douglas-fir trees form small, rather dense groves or exist as scattered individuals. Occasionally, the lower slopes of entire hillsides abound with this species, but more commonly stand size is about 0.1 ha.

Where bigcone Douglas-fir regeneration was found, seedling density ranged from 138 to 1027 per ha, with an average of 326. Advance repro-

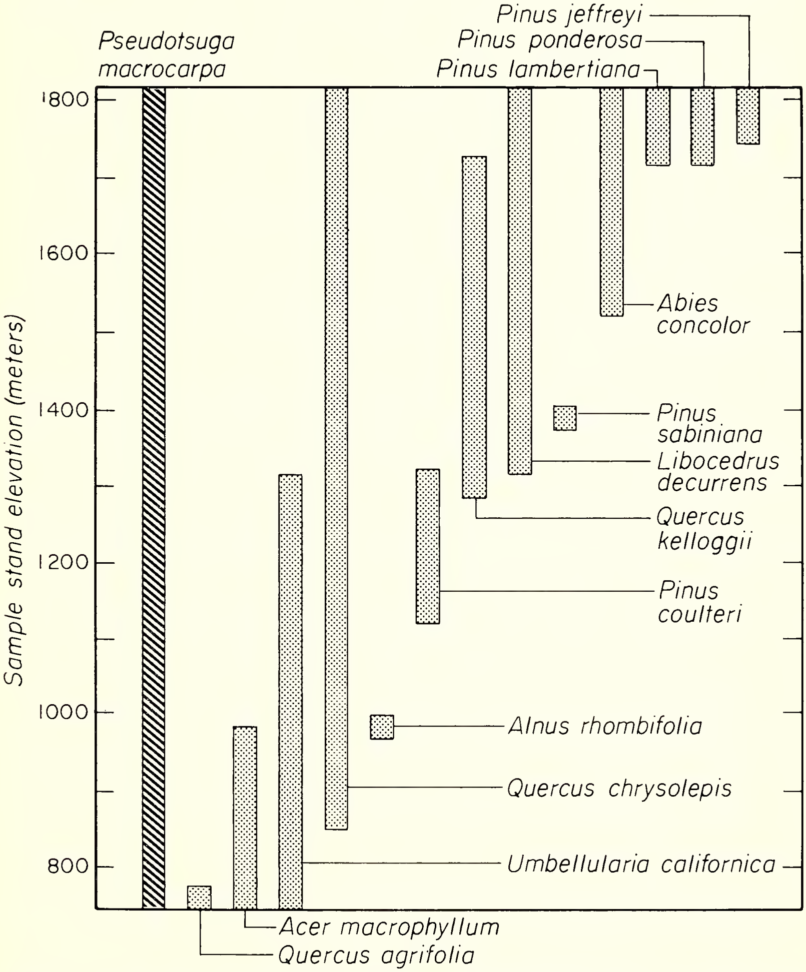

FIG. 2. Elevational distribution of bigcone Douglas-fir, canyon live oak, and other tree associates within sampled bigcone Douglas-fir range.

duction had a near-similar mean and range in density. The tree category ranged from 2.8 to 137.2 cm d.b.h. Its density varied from 20 to 662 and averaged 267 trees per ha. Examination of these values indicated that bigcone Douglas-fir seedlings, advance reproduction, and trees were evenly distributed along the elevational gradient.

Of the 16 stands, the best-represented diameter class for bigcone Douglas-fir was the largest class, and the poorest was the regeneration class (Table 1). Furthermore, each stand included at least two diameter classes, several five; the average was four.

The basal area of bigcone Douglas-fir trees exceeding 2.5 cm d.b.h. ranged from about 5 m^2 per ha to about 253 m^2. The number of stems was inversely related to basal area: the smallest number of stems occurred in the largest diameter classes, which in turn had the highest basal areas. This was particularly true of stands with trees 50.9 cm in diameter and larger.

Where canyon live oak regeneration was present, its density ranged from 20 to 1570, averaging 365 seedlings per ha. Canyon live oak regeneration was found in five of the six stands having bigcone Douglas-fir regeneration. Canyon live oak advance reproduction averaged 345 plants per ha, and occurred in 7 of the 8 stands having bigcone Douglas-fir advance reproduction. The density of canyon live oak trees in the diameter range of 2.8 to 91.4 cm ranged from 20 to 1423 with an average of 395 plants per ha. Further examination showed that canyon live oak seedlings, advance reproduction, and trees were evenly distributed along the elevational gradient.

In the 16 stands, canyon live oak was best represented in the 4 smallest diameter classes and poorly represented in the 3 largest classes (Table 2). This representation is almost the exact opposite of bigcone Douglas-fir.

Each stand was analyzed further to ascertain the number of diameter classes in each. They ranged from none to six. The average was four—the same as for bigcone Douglas-fir.

Basal area of canyon live oak ranged from 1 to 124 m^2 per ha. It exceeded the basal area of bigcone Douglas-fir through the 2.8- to 50.8-cm

TABLE 1. DIAMETER CLASS REPRESENTATIONS IN SAMPLES FROM SIXTEEN STANDS OF BIGCONE DOUGLAS-FIR.

Diameter class (cm)	Number of stands where diameter class is present
Regeneration	6
Advance reproduction	8
2.8 – 10.2	9
10.3 – 30.5	11
30.6 – 50.8	9
50.9 – 76.2	7
76.3+	13

TABLE 2. DIAMETER CLASS REPRESENTATIONS IN SAMPLES FROM SIXTEEN STANDS OF CANYON LIVE OAK.

Diameter class (cm)	Number of stands where diameter class is present
Regeneration	12
Advance reproduction	13
2.8 – 10.2	10
10.3 – 30.5	13
30.6 – 50.8	5
50.9 – 76.2	6
76.3+	5

diameter class, equalled it in the 51.1- to 76.2-cm class, and was only one-third of it in the largest diameter class. Canyon live oak basal area was less than bigcone Douglas-fir in 11 of the 15 stands where both grew. The magnitude of difference was over two to one in favor of bigcone Douglas-fir. A paired "t" test (Snedecor, 1956) of the two species indicated a significant difference in basal areas at the 1 percent level of probability.

Regeneration of associated species was noted in seven stands. Of these species, *Quercus kelloggii* was most successful, regenerating in four stands; *Umbellularia californica* was present in three. Where present, regeneration of associated species averaged 119 plants per ha. For advance regeneration, which was observed in ten stands, *Umbellularia californica* grew in five stands and *Libocedrus decurrens* in three stands. Average density for advance reproduction was about 168 plants per ha and rarely included more than three species.

Tree density of associated species ranged from 49 to 850 stems per ha, but densities of individual species ranged from 49 to 326 with an average of 109.

Tree associates of bigcone Douglas-fir were not as widespread as it in terms of elevation. Presence of each species was calculated as a percentage of the 16 sampled stands (Table 3).

Aggregate basal area of the associated species ranged from 1 to 40 m^2 per ha. Average values were intermediate between those of bigcone Douglas-fir and canyon live oak up to 50.8 cm in diameter, and less than either species above this diameter. Placement along the elevational gradient yielded no meaningful trends for basal area or density.

High and low basal area values for bigcone Douglas-fir, canyon live oak, and associated species in each diameter class were randomly dispersed along the gradient.

Basal areas indicate not only relative diameters but also the extent that a given area is occupied by trees. For all tree species combined, stand basal area ranged from 40 to 293 m^2 per ha, averaging 126 m^2.

Members of the woody shrub genera *Arctostaphylos, Ceanothus, Rhamnus, Ribes,* and *Rhus* are almost totally lacking beneath the big-

TABLE 3. PRESENCE OF TREE SPECIES ASSOCIATED WITH BIGCONE DOUGLAS-FIR. Presence is expressed as a percent of 16 stands in which the species occurred.

Species	Percent	Species	Percent
Quercus chrysolepis	94	*Pinus lambertiana*	12
Umbellularia californica	44	*Pinus ponderosa*	12
Libocedrus decurrens	44	*Quercus agrifolia*	6
Quercus kelloggii	38	*Alnus rhombifolia*	6
Acer macrophyllum	25	*Pinus sabiniana*	6
Abies concolor	25	*Pinus jeffreyi*	6
Pinus coulteri	19		

cone Douglas-fir stands. But because these shrubs are often located on the fringes of the sample stands, many seeds undoubtedly are in the upper soil (Quick, 1956).

Slope and Aspect Gradients. The 16 stands were arranged along slope and aspect gradients by plotting density and basal area. No trends materialized for bigcone Douglas-fir, canyon live oak, or associated species.

The interaction of aspect and elevation, however, seemed to govern the occurrence of bigcone Douglas-fir. At lower elevations, this species grows near streams in moist, shaded canyons and draws, where aspects are mostly north and east. As elevation increases from 1350 to 1700 m, aspects broaden to include more south- and southeast-facing slopes. At these higher elevations, benches, sloping hillsides, and ridges often are clothed with this species. At bigcone Douglas-fir's highest elevational zone (over 1700 m), it is found on warmer south and west aspects without regard to canyons, streams, and draws.

Available Moisture Gradient. Numerous factors were considered in establishing the moisture gradient. In order of magnitude they were: (1) presence of a permanent stream; (2) presence of an ephemeral stream; (3) degree of moisture stress in trees as noted by Griffin (1967), Waring (1969), and Wilson and Vogl (1965); and (4) aspect, slope, and elevation. On the basis of these factors, four stands were rated as xeric, three as moderately xeric, three as moderately mesic, and six as mesic. Among these habitats, density and basal area by species were then compared.

Bigcone Douglas-fir and canyon live oak regeneration and advance reproduction were present in all habitats. Both species in both size classes were more dense, however, in stands rated as xeric or moderately xeric. Bigcone Douglas-fir and canyon live oak trees were well represented in all habitats. No trends in density or basal area were identified.

Soil Depth and Latitudinal Gradients. Soil parent materials generally belonged to two classes—granitics and metasedimentaries (sandstone and schist). Of the 16 sampled stands, four grew on metasedimentary parent materials, ten on granitics, and two in contact zones where the parent material was primarily granitic. Tentative soil series on metasedimentary material were Laughlin and Friant; in contact zones, Oak Glen; and on granitics, Tollhouse, Cieneba, Crouch, and two others that resembled Tish Tang and Neuns.

In general, soils showed a broad range of depth and development. Some were shallow and poorly developed, others were deep and better developed. Nearly all, however, were coarse textured and well drained.

Arraying density and basal area by species and size classes along soil depth and latitudinal gradients showed no trends. Within the study area, changes in latitude and soils scarcely affect the stability and site preference of bigcone Douglas-fir. The possibility exists that added moisture and cooler temperatures resulting from fog in the Santa Ana and Agua Tibia Mountains might benefit bigcone Douglas-fir. But since no differences were found along the latitudinal gradient, fog apparently is not a meaningful factor.

Discussion

Evidence is strong that the sample stands have been free of major disturbance for many years. That both bigcone Douglas-fir and canyon live oak average four diameter classes per stand and that the usually abundant woody shrub species are absent support this thought. Thus, regeneration, advance reproduction, and tree data, as presented, are representative of stand development in an undisturbed state.

Although bigcone Douglas-fir and canyon live oak associate closely, similarities and differences exist among seedlings, advance reproduction, and trees. Average densities of seedlings and advance reproduction of both species are similar. When combined for both species, average density is 1324 plants per ha. For trees smaller than 30.5 cm in diameter, canyon live oak is more dense; for those above 30.5 cm, bigcone Douglas-fir density rates highest. A generally similar and statistically significant relationship between the two species also holds for basal area.

Canyon live oak's poorer representation in the larger diameter classes probably results from a combination of environmental and genetic factors. Because canyon live oak sprouts from the root crown after fire or other damage, it often produces clones. With fire commonplace throughout the mountains of southern California (Wilson and Vogl, 1965; Wright, 1966; Vogl and Miller, 1968), most of the hardwoods are clonal and have three to five stems per clone. Individual trees within these clones seldom reach 76.2 cm in diameter.

Another strong relationship is the ability of bigcone Douglas-fir regeneration and advance reproduction to grow under dense stands of canyon live oak or of both species. Where basal area levels are high, however, regeneration of bigcone Douglas-fir generally is absent.

In addition to canyon live oak, other species of trees also reside within the sampled range of bigcone Douglas-fir. The degree of occurrence of individual species (presence) is low, however, and ranges from 6 to 44 percent. Most often, these tree associates and their regeneration are less numerous than bigcone Douglas-fir and canyon live oak, and their overall basal area is much lower. While an integral part of most stands, they do not appear to threaten domination of any stand.

Taken together, all factors studied demonstrate the existence of an ecological unit, the bigcone Douglas-fir–canyon live oak community. This community in the forests of southern California is distinguished principally by its remarkable ecological stability. Several characteristics emphasize this stability:

1. Both species are long-lived and relatively large.
2. Both species have only moderate reproductive potential and rather limited seed dispersal. Seed crops are infrequent for bigcone Douglas-fir (Gause, 1966). While seed crops are more frequent for canyon live oak, a high proportion of acorns often are infertile.
3. Early seedling growth of both species is slow, enabling large numbers of seedlings to accumulate.
4. Seedlings show little seedbed preference but do best under an overstory or on the shaded overstory fringes.
5. Both species grow rather slowly, although bigcone Douglas-fir accelerates growth after reaching above the oak overstory.
6. Both species possess strong survival mechanisms, chiefly sprouting ability. This characteristic is unusual for a North American conifer.

Because of this stability, the areal extent of the bigcone Douglas-fir–canyon live oak community will change little, if any. If changes do take place, they will occur within the community. The two principal species, having similar ecological characteristics, are probably in dynamic equilibrium. Shifts in this equilibrium result from major disturbances, primarily fire.

By knowing the autecology of the species in the community, and by carefully observing stand structure and species composition of many stands, a trained observer can put together a developmental sequence for undisturbed and disturbed stands.

With continued exclusion of fire, bigcone Douglas-fir seedlings beneath the canyon live oak canopy eventually grow through it and dominate. Fir seedlings on the fringes of undisturbed oak stands also become dominant. Therefore, with the absence of fire, fir trees eventually replace the oaks and dominate the community. This is a slow steady process, however, and results in only minor changes in stand composition and structure.

When the community burns, all but the largest bigcone Douglas-firs are killed. Large trees live by resprouting along the boles, but their ability to produce seed is impaired for years. Thus, after fire, bigcone Douglas-fir in the community is limited to large sizes. Most burned canyon live oaks promptly sprout from root crowns. So do oak seedlings and advance reproduction on the forest floor. Thus presence of canyon live oak in the community is relegated to the smaller size classes.

With or without fire, additional area lost or gained by the community is likely to be small.

The overall pattern of the bigcone Douglas-fir–canyon live oak community is that of a stable, self-perpetuating, somewhat exclusive community, with tendencies toward the climax or even postclimax successional stage. Weaver and Clements (1938) implied that the postclimax community is usually a relict community as well. Such a community would exist in an area where the local climate, topography, or soil would compensate for the aridity of modern, as contrasted to Miocene, times. Vegetation in gorges, canyons, and "long and steep slope exposures" qualified under the Weaver and Clements definition of postclimax. Certainly these conditions typify the habitat of the present-day bigcone Douglas-fir–canyon live oak community. Indeed, Cooper (1922) called the entire broad sclerophyll forest, of which this community is a part, postclimax.

Axelrod (1937) and Mason (1940) found evidence of a progenitor of bigcone Douglas-fir in both the Pliocene and Pleistocene epochs. Fossil specimens similar to *Quercus chrysolepis* and *Q. agrifolia, Pinus coulteri* and *P. sabiniana,* and *Sequoia* spp. of today also were found in association. That the bigcone Douglas-fir–canyon live oak community is a relict community is likely.

An almost complete lack of correlation exists between this community and the variables quantified in this study. Edaphic and physiographic variables were particularly unimportant—at least at the magnitude of sampling used. Most of the many combinations of slope, aspect, soil, and elevation examined similarly support the bigcone Douglas-fir–canyon live oak community. This suggests that, as individual factors vary among the stands, they complement each other and, together, provide environments that are nearly alike biologically. Thus the community seems to be narrowly endemic, occupying a specific habitat in the canyons and on the slopes of mountainous southern California.

In California's Santa Ana mountains, Bolton and Vogl (1969) found that "bigcone Douglas-fir will continue to occupy the same relative position to other vegetation types in the future, and that only by rapid environmental changes can it be reduced or increased from its present status". This work supports their finding and extends it to most of the natural range of the species.

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MEXICAN SPECIES OF ABUTILON SECT. ARMATA (MALVACEAE), INCLUDING DESCRIPTIONS OF THREE NEW SPECIES

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Abutilon Mill. sect. *Armata* Presl is a natural group. Critical revision of the entire genus, including typification and evaluation of the approximately 25 infrageneric groups that have been named, may lead to the conclusion that this taxon should have another name and/or different rank; the group is thus accepted only provisionally as sect. *Armata.*

Characteristic features of this taxon include robust growth habit,